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Review

# Worldwide decline of the entomofauna: A review of its drivers

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ABSTRACT

Biodiversity of insects is threatened worldwide. Here, we present a comprehensive review of 73 historical reports of insect declines from across the globe, and systematically assess the underlying drivers. Our work reveals dramatic rates of decline that may lead to the extinction of 40% of the world's insect species over the next few decades. In terrestrial ecosystems, Lepidoptera, Hymenoptera and dung beetles (Coleoptera) appear to be the taxa most affected, whereas four major aquatic taxa (Odonata, Plecoptera, Trichoptera and Ephemeroptera) have already lost a considerable proportion of species. Affected insect groups not only include specialists that occupy particular ecological niches, but also many common and generalist species. Concurrently, the abundance of a small number of species is increasing; these are all adaptable, generalist species that are occupying the vacant niches left by the ones declining. Among aquatic insects, habitat and dietary generalists, and pollutant-tolerant species are replacing the large biodiversity losses experienced in waters within agricultural and urban settings. The main drivers of species declines appear to be in order of importance: i) habitat loss and conversion to intensive agriculture and urbanisation; ii) pollution, mainly that by synthetic pesticides and fertilisers; iii) biological factors, including pathogens and introduced species; and iv) climate change. The latter factor is particularly important in tropical regions, but only affects a minority of species in colder climes and mountain settings of temperate zones. A rethinking of current agricultural practices, in particular a serious reduction in pesticide usage and its substitution with more sustainable, ecologically-based practices, is urgently needed to slow or reverse current trends, allow the recovery of declining insect populations and safeguard the vital ecosystem services they provide. In addition, effective remediation technologies should be applied to clean polluted waters in both agricultural and urban environments.

## 1. Introduction

For years, biologists and ecologists have been concerned about the worldwide reduction in biodiversity undergone by many terrestrial and aquatic vertebrates (Ceballos and Ehrlich, 2002; Pimm and Raven, 2000; Wilson, 2002), yet scientists have only recently voiced similar concerns about invertebrate taxa, particularly insects. Population declines imply not only less abundance but also a more restricted geographical distribution of species, and represent the first step towards extinction (Diamond, 1989). Much of the blame for biodiversity loss falls on human activities such as hunting and habitat loss through deforestation, agricultural expansion and intensification, industrialisation and urbanisation (Ceballos et al., 2017; Maxwell et al., 2016), which jointly claimed a 30–50% encroachment on natural ecosystems at the end of the 20th century (Vitousek et al., 1997).

There is compelling evidence that agricultural intensification is the main driver of population declines in unrelated taxa such as birds, insectivorous mammals and insects. In rural landscapes across the globe, the steady removal of natural habitat elements (e.g. hedgerows), elimination of natural drainage systems and other landscape features together with the recurrent use of chemical fertilisers and pesticides negatively affect overall biodiversity (Fuller et al., 1995; Newton, 2004; Tilman et al., 2001). Recent analyses point to the extensive usage of pesticides as primary factor responsible for the decline of birds in grasslands (Mineau and Whiteside, 2013) and aquatic organisms in streams (Beketov et al., 2013), with other factors contributing to or amplifying their effects to varying extent. Yet, we don't know whether the same factors explain the parallel entomological demise that we are witnessing.

In 2017, a 27-year long population monitoring study revealed a

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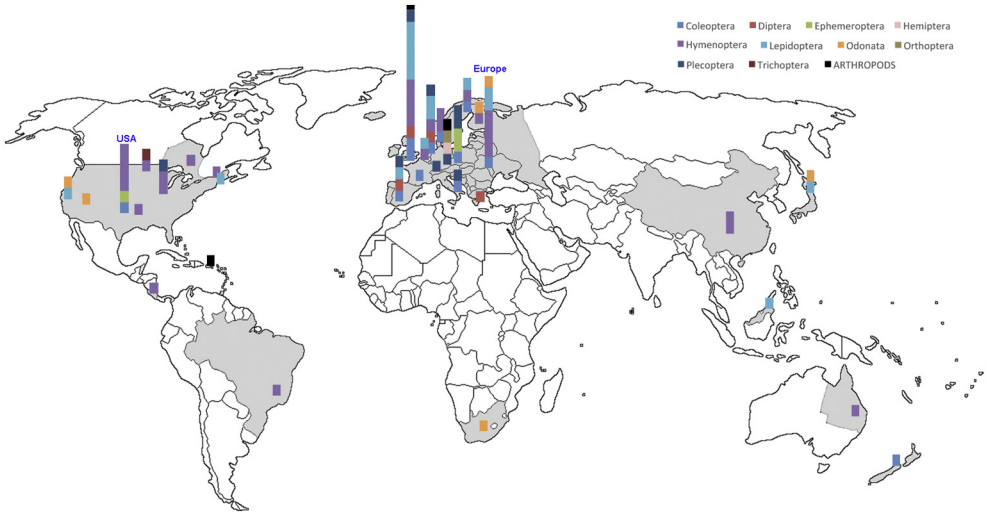


**Fig. 1.** Geographic location of the 73 reports studied on the world map. Columns show the relative proportion of surveys for each taxa as indicated by different colours in the legend. Data for China and Queensland (Australia) refer to managed honey bees only. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

shocking 76% decline in flying insect biomass at several of Germany's protected areas (Hallmann et al., 2017). This represents an average 2.8% loss in insect biomass per year in habitats subject to rather low levels of human disturbance, which could either be undetectable or regarded statistically non-significant if measurements were carried out over shorter time frames. Worryingly, the study shows a steady declining trend over nearly three decades. A more recent study in rainforests of Puerto Rico has reported biomass losses between 98% and 78% for ground-foraging and canopy-dwelling arthropods over a 36-year period, with respective annual losses between 2.7% and 2.2% (Lister and Garcia, 2018). The latter authors showed parallel declines in birds, frogs and lizards at the same areas as a result of invertebrate food shortages. Both studies agree with the declining trend in flying insects (mainly Diptera) observed a decade earlier in parts of Southern Britain (Shortall et al., 2009). As insects comprise about two thirds of all terrestrial species on Earth, the above trends confirm that the sixth major extinction event is profoundly impacting life forms on our planet (Thomas et al., 2004).

While the arthropod declines in tropical rainforests correlate well with climatic changes, the 12 different factors (e.g. increases in arable land, deforestation, global warming) that were thought to be responsible for year-to-year drops in insect biomass in Germany barely accounted for ~20% of observed declines. Rather surprisingly, 80% of observed inter-annual variability in insect numbers was left unexplained (Hallmann et al., 2017). Although the authors did not assess the effect of synthetic pesticides, they did point to them as a likely driver of the pervasive losses in insect biomass.

The above studies, however, are in line with previous reports on population declines among numerous insect taxa (i.e. butterflies, ground beetles, ladybirds, dragonflies, stoneflies and wild bees) in Europe and North America over the past decades. It appears that insect declines are substantially greater than those observed in birds or plants over the same time periods (Thomas et al., 2004), and this could trigger wide-ranging cascading effects within several of the world's ecosystems.

This review summarises our current state of knowledge about insect declines, i.e., the changes in species richness (biodiversity) and population abundance through time, and points to the likely drivers of the losses so that conservation strategies to mitigate or even reverse them may be implemented. Previous reviews are partial in scope, restricted to individual groups of insects (e.g. butterflies, carabids) in specific regions, but no study has put together a comprehensive review of all insect taxa nor compared the local findings among different parts of the world.

## 2. Methodology

We aimed at compiling all long-term insect surveys conducted over the past 40 years that are available through global peer-reviewed literature databases. To that effect we performed a search on the online Web of Science database using the keywords [insect*] AND [declin*] AND [survey], which resulted in a total of 653 publications. The majority of these referred to Hymenoptera (55), Diptera (45), Coleoptera (44) and Lepidoptera (37) taxa, among which only a few dealt with long-term surveys. Reports that focused on individual species, pest outbreaks or invasive species were excluded. We selected surveys that considered all species in a taxon (e.g. family or order) within large areas (i.e. a region, a country) or smaller areas surveyed intensively over periods longer than 10years. Additional papers were obtained from the literature references. Finally, only surveys that reported changes in quantitative data over time, either species richness or abundance, were considered. Thus, this review covers 73 reports on entomofauna declines in various parts of the world (Fig. 1) and examines their likely causes (Table S1). Because the overwhelming majority of long-term surveys have been conducted in developed countries, particularly in the northern hemisphere, this review is geographically biased and does not adequately cover trends in tropical regions, where information on insect biodiversity is either incomplete or lacking (Collen et al., 2008).

The above literature records use accurate scientific data on species distribution from museum specimens (56%), which are compared with long-term survey data obtained decades later (72%), and sometimes rely upon citizen science data (8%). Because the latter data tend to overestimate the diversity of insects due to over-reporting of rare species (Gardiner et al., 2012), the overall assessment of biodiversity can be considered conservative.

Conservation status of individual species follows the IUCN classification criteria (IUCN 2009): threatened species include vulnerable (> 30% decline), endangered (> 50%) and critically endangered (> 75% decline) species. Data on population abundance are more difficult to obtain than geographical distribution records, but a few reports quantified the extent of such declines for Lepidoptera, Hymenoptera and dung beetles (Coleoptera). An annual rate of decline (percentage of species declining per year) was estimated for each taxon and region.

A meta-analysis of the declines among the various taxa and regions was performed, with groups compared using analysis of variance (ANOVA). Enumerated drivers of the declines -as indicated by the reports' authors- are tabulated and analysed, and further discussed with reference to experimental and other empirical data available in the literature.

## 3. Taxa declines

### 3.1. Lepidoptera

Butterflies and moths are valuable indicators of environmental quality, considering their high degree of host-plant specialisation and vulnerability to habitat deterioration (Erhardt and Thomas, 1991). Given their presence in a broad range of habitats, the loss of Lepidoptera may directly impact the delivery of key ecosystem services such as pollination and natural pest control (Fox, 2013). Moths, which are about 10 times more diverse than butterflies, constitute important prey items of bats and help sustain population levels of myriad other insectivorous animals (Hahn et al., 2015; Vaughan, 2008; Wilson et al., 1999).

Maes and van Dyck (2001) were the first to report drastic changes in butterfly biodiversity in Flanders (Belgium) during the 20th century, including the extinction of 19 (out of 64) native species since 1834. Habitat loss resulted in a steady decline of 69% of the 45 extant species, while the extinction rate increased from 0.2 to 1.7 species/5-year since 1950 as urbanisation and agricultural intensification expanded eightfold (Maes and Van Dyck, 2001). A follow-up study in the Netherlands found that 11 of the 20 most common and widespread butterfly species declined both in distribution and abundance between 1992 and 2007, whereas populations of species associated with natural habitats in nature reserves remained stable. Local populations of *Lasiommata megera* and *Gonepteryx rhamni* are now endangered and two other species (*Aglais io* and *Thymelicus lineola*) are vulnerable (van Dyck et al., 2009). In parallel, the range of distribution of 733 species of day-flying moths was recorded between 1980 and 2000: overall declines were observed in 85% of species, 38% of them experiencing > 75% reduction in their area (i.e. critically endangered), 34% being considered threatened and 15% vulnerable (Groenendijk and van der Meulen, 2004). In particular, 47 of the 55 species monitored in peat-bog marshes declined, six remained stable and only two (*Plusia putnami* and *Deltote bankiana*) increased in range (Groenendijk and Ellis, 2011). The most affected species are those with lower dispersal abilities and preference for oligotrophic habitats.

Among the 269 species of macro-lepidopterans monitored for 50 years at the Kullaberg Nature Reserve (Sweden), 45% were declining, 22 were coloniser species and 159 were no longer found in 2004 (Franzén and Johannesson, 2007). Monophagous and oligophagous species using grass or herbs in wetlands were declining more than those feeding on deciduous trees or shrubs, confirming that dietary specialists bear the brunt of the declines. Species with a short flight-period or those restricted to non-forest habitats were all associated with a high extinction risk. A comparison of historical records of 74 butterflies in Finland showed how 60% of grassland species declined over the past 50 years, whereas 86% of generalist species and 56% of those living at forest edge ecotones increased in abundance (Kuussaari et al., 2007). Common traits of the 23 declining species are a reduced mobility, oligotrophic habitat preference and seasonal migration behaviour. Another study on the populations of 306 species of noctuid moths in Finland over 1988–1997 reported the greatest declines for species with comparatively small geographic range, whereas polyphagous moths with longer flight periods and those that overwintered as adults had the widest distributions (Mattila et al., 2006). By contrast, species that overwintered as either larval or pupal stages suffered the largest declines over that period.

Similar findings were reported for north-eastern Spain, where yearly monitoring of 183 butterfly species over 1994–2014 permitted an in-depth analysis of population trends and associated factors for 66 species. While 15 species had increased in abundance, five remain stable and 46 are declining (Melero et al., 2016). Although the extent of species decline did not differ among seven habitat types selected, forest butterflies appeared to be declining faster than those from other habitats due mainly to specialisation of the larval trophic stage and multivoltinism.

A comprehensive report on the status of 576 species of butterflies in Europe found that 71 were threatened and declined over a 25-year period (van Swaay et al., 2006). The largest declines occurred among specialist butterflies of grassland biotopes (19% species), wetlands and bogs (15%) and woodlands/forests (14%), due to habitat conversion into crops and the adoption of intensive agricultural practices, e.g. fertilisers and pesticides negatively affected 80% species. Some species (*Lopinga achine* and *Parnassius apollo*) had declined due to afforestation, i.e. conversion of open woodland habitats to dense forests. Climate change only affected a few endemic species adapted to mountainous biotopes. A more recent assessment of 435 butterflies native to Europe (van Swaay et al., 2010) found that populations of 19% of species are declining, particularly in Mediterranean and eastern countries, 8.5% species are threatened, and three are critically-endangered, i.e. *Pieris brassicae wollastoni*, *Triphysa phryne* and *Pseudochazara cingovskii*. Belgium and the Netherlands are the European countries with the highest losses of butterfly biodiversity (19 and 17 country-level extinctions, respectively), whereas Denmark and the U.K. have the least (4 species extinct each) (Maes and Van Dyck, 2001). One species (*Aricia hyacinthus*) is considered extinct over the European continent.

Butterflies appear to be declining faster in the United Kingdom, as 74% of 46 non-migratory butterflies restricted their distribution over 1970–1999 (Warren et al., 2001). Using a comprehensive database compiled by amateur collectors and scientists over a 29-year period in the entire British Isles, the authors showed that habitat specialists experienced the largest reductions in distributional area. Specialist and sedentary species not showing changes in abundance over 25 years had reduced their distribution on average by 15%. Other studies indicate that 41 out of 54 common butterflies had been declining since the 1970s, with 26% of species showing decreases over 40% of their range (Fox et al., 2006), while 13% of 10-km squares in the monitoring grid reported disappearance of butterfly species (Thomas et al., 2004). Although authors did not attempt to correlate the declines with specific drivers, the following combination of factors was suggested: habitat fragmentation and/or destruction, intensification of agriculture, including the increased usage of chemical fertiliser and pesticides, and perhaps over-collecting – although such practice has been greatly reduced by more environmental awareness. To minimise biodiversity losses among butterflies and moths, the UK Butterfly Monitoring Scheme (UKBMS) was created, which compiles data on the abundance and distribution of all species across the country since 1976. An initial analysis of 50 species showed a large fluctuation in butterflies among years, with specialist species having declined by 34% nationally since the scheme was established; generalist species had declined in England (12%) but little (6%) or not at all in Scotland. Major declines occurred in forests and farmland regardless of the efforts to restore biodiversity from 2000 onwards (Brereton et al., 2011). A further analysis of 17 widespread and resident species of butterflies between 1984 and 2012 showed that abundance of all species decreased by 58% since the year 2000, while 15 species exhibited population declines at average annual rates between −0.8% and −6.7% (Gilburn et al., 2015). Thus, 41% of the species studied are threatened. Increasing summer temperatures had a marked positive effect on butterfly abundance, whereas none of the other climatic factors could explain the decrease in their populations. By contrast, the steepest declines occurred in areas with high proportions of farmland treated with neonicotinoid insecticides; indices for the 15 declining species showed negative associations with neonicotinoid usage.

Similar rates of decline were reported among 337 moth species throughout England between 1968 and 2003: 222 showed declining populations over the 35-year study period, with a median 10-yr population decrease of 12%, although decreases were larger in the south of the country (17%) compared to the north (5%) (Conrad et al., 2006). The larger declining trends in the south were associated with the degree of agricultural intensification, as also recorded at Rothamstead between

the 1940s and 1960s (Woiwod & Gould, 2008 cited in Fox, 2013). At that time, 71 species of moths were considered threatened, 58 were vulnerable and 13 endangered. Subsequent surveys of about 900 species of moths by experts and amateurs over 25 years corroborated the previous findings, with decreases in range size for moths mirroring those of butterflies (Fox et al., 2011). Notable declines were recorded for *Macaria wauaria* (77% decrease) *Graphiphora augur* and *Dasypolia templi* (> 45% each), which are now included in the country's Red List, while decreases of *M. wauaria* and *Eulithis mellinata* were likely due to insecticide use on their host plants (i.e., currants). A northward shift of 12 common moth species showed that these insects were moving at 7.8 km/year since 1985. Species such as *Katha depressa*, *Idaea rusticata* and *Collita griseola* have each doubled their distribution and spread northwards by approximately 100 km. Some moths extended their range as a result of the widespread cultivation of their host plants in gardens or commercial conifer plantations.

For the United States, long-term monitoring data of butterflies are limited. Surveys in prairie habitats and bogs of Wisconsin and Iowa over 2002–2013 indicate fluctuating populations of certain species, but lack of consistency prevents drawing temporal trends. Main drivers appear to be habitat modification and moisture levels dependent on climate change (Swengel et al., 2011; Swengel and Swengel, 2015). In Massachusetts, the distributional ranges of 116 species shifted northwards between 1992 and 2010. Two southern species adapted to warmer conditions expanded in range (*Papilio cresphontes* and *Poanes zabulon*), while populations of 80% of butterflies declined in southern parts of that State; the only trait that correlated significantly with the declines was the overwintering stage of each species (Breed et al., 2012). In California, surveys on presence/absence of 67 butterfly species at four sites between 1972 and 2012 revealed that the average number of species at any site (30) remained stable until 1997, but dropped steeply to 23 in the last year of the study. The overall trend implies that 23% of species are disappearing. Data on species richness were correlated to annual variables such as summer temperatures, percentage of land converted to agriculture and usage rates of different insecticide classes. Only the latter two variables showed a significant correlation with the observed declines, and within the pesticides only neonicotinoid usage showed a positive correlation; incidentally, the start of the declining trend in 1997 followed the introduction of these systemic insecticides in that State in 1995 (Forister et al., 2016).

Although survey records are limited, Lepidoptera declines appear to be less dramatic in certain parts of the Asian region. In Japan, 15% of the 240 species of butterflies are threatened, but among those 80% of the grassland species are endangered, with two species close to extinction in the national territory: *Melitaea scotosia* (98% decline) and *Argynnis nerippe* (95% decline) (Nakamura, 2011). At the individual island level, seven species are now extinct. Species of the woodlands (40) are the most stable, while the steady intensification of Japan's traditional “satoyama” landscape (i.e., a mosaic of rice paddy fields, grassland and coppice forests) has negatively affected most species. Collecting of specimens was also as a minor driver after 1990. In Malaysia, some 19% of moths at Mount Kinabalu (Borneo) had their abundance reduced between 1965 and 2007 (Chen et al., 2011). Species typical of high altitudes (28) have shrunk their range as they shifted some 300 m uphill, whereas a third of the moths expanded their upper boundary upward by 152 m and retreated their lower boundary by 77 m as a result of global warming during the 40-year period.

### 3.2. Hymenoptera

Bees are essential pollinators of flowering plants, accounting for a third of all pollinators (Ollerton et al., 2011) and honey bees have been managed for millennia as a source of honey and beeswax. Knowledge about their population status, therefore, is important for the ecosystem services they provide as well as their economic value (Gallai et al., 2009). However, the status of most other hymenopterans – i.e., ants, wasps and parasitoids; several of which provide equally important ecosystem services – remains practically unknown to this date.

#### 3.2.1. Bumblebees (Bombus spp., Apidae)

The first report on the status of 18 bumblebees in Britain, using a numerical approach on a national map grid, showed declining trends for seven species since the 1960s, with large reductions in the range of four species (i.e., *Bombus humillis*, *B. ruderatus*, *B. subterraneus* and *B. sylvarum*) in the southern and central parts of England (Williams, 1982). An analysis of the causal factors responsible for such declines, using foraging data on eight native bumblebees and information on their distribution, found that the species subject to the greatest reduction in distribution were host-plant specialists. Thus, bumblebees that forage on grasslands and farmland flowers underwent the largest reductions. Particularly, three species of long-tongued bumblebees (*B. humillis*, *B. ruderatus* and *B. subterraneus*) that forage on clover and other legumes, traditionally used in rotations as a source of nitrogen, had their populations curtailed after the foraging plants were steadily replaced by chemical fertilisers in southern England (Goulson et al., 2005). By contrast, short-tongued bumblebees remain common in gardens and urban areas where they have access to a large array of native and introduced flowers.

In Denmark, long-tongued bumblebee species have declined in richness and abundance since the 1930s, particularly during the red-clover flowering season, while short-tongued species were unaffected. Five out of the original 12 species present eight decades earlier were absent, all long-tongued species, and the once common *B. distinguendus* is now endangered. Only *B. pascuorum* seemed to be increasing in abundance, possibly by occupying some of the niches left vacant by declining species (Dupont et al., 2011). A larger study of 60 species and subspecies of bumblebees in central Europe found that 48 have declined in abundance over the past 136 years, with 30% of them being considered threatened and four having become extinct (Kosior et al., 2007). Most of the country extinctions occurred in the second half of the 20th century, coinciding with the expansion of agricultural intensification brought about by the Green Revolution. The abundance of pollinators in Swedish red clover fields also declined dramatically since 1940, with only two rare species remaining stable while two short-tongued generalist species now dominate the landscape: *B. terrestris* and *B. lapidarius* (Bommarco et al., 2012). Such a dramatic change in relative abundance has negatively affected the yields of that crop, which depends entirely on pollination services of long-tongued species. As in Denmark, *B. distinguendus* has completely disappeared from the southern part of Sweden. Large-scale conversion of landscapes to intensive agriculture together with unrelenting pesticide use are blamed for the changes in bumblebee biodiversity observed over the past 75 years (Bommarco et al., 2013). Major declining trends were identified among 46% of all *Bombus* species in Europe, of which 24% are threatened and one (*B. callumanns*) shows > 80% decline due mainly to habitat fragmentation and the replacement of clover with chemical fertilisers in agricultural areas (Rasmont 2005 cited by Nieto et al., 2014).

Several large studies have been conducted in North America to assess the status of bumblebee populations and their temporal and spatial changes in that continent since the middle of the 19th century. Half of the 14 species of bumblebees surveyed in southern Ontario (Canada) between 1971 and 2006 were declining, three were increasing (*B. bimaculatus*, *B. impatients and B. rufocintus*) while another three could not be found in that period: *B. affinis*, *B. pensylvanicus and B. terricola* (Colla and Packer, 2008). Higher tolerance to pesticides could explain the expansion of the three most abundant species at the expense of the more sensitive species, which had practically disappeared from the region. The Xerces Society reported losses of bumblebees in northern California and southern Oregon in 2005 and blamed the pathogen microsporidian *Nosema bombi* for most of the declines (Thorp and Shepherd, 2005). Using museum records from the Illinois Natural History Survey for the period 1900 to 2007, the distributional range of 16

species of bumblebees were analysed. Half of them have declined in numbers, whereas four species have become extinct in midwestern regions: *B. borealis*, *B. ternarius*, *B. terricola* and *B. variabilis*. The main reductions occurred during 1940–1960, coinciding with the expansion of intensive agriculture and increases in pesticide use (Grixti et al., 2009). At a national scale, changes in the distribution of eight bumblebee species could be determined by comparing historical records with intensive surveys across 382 locations in the USA. Half of the species declined in abundance by as much as 96% of their initial populations only in the last 30 years, and their geographical range was reduced between 23 and 87%. Declines were blamed on reduced floral and nesting resources, but declining populations also had greater infection rates by *N. bombi* and lower genetic diversity than the non-declining bee populations; some of the sharpest declines were recorded in regions dominated by intensive agriculture (Cameron et al., 2011). In Oklahoma, only five of the 10 species of bumblebees that were present in 1949 were found in 2013 after extensive surveys in 21 counties. Contrasting with other States, *B. pensylvanicus* was the most common species, whereas *B. variabilis* is presumed extinct (Figueroa and Bergey, 2015). In the latest study to date, historical records of 16 species of bumblebees in the eastern USA (New Hampshire) over 1866–2015 were analysed. Nine species have been declining, including five that are presently threatened: *B. ashtoni*, *B. fernaldae*, *B. rufocintus*, *B. pensylvanicus* and *B. sandersoni*. One species, *B. terricola*, was found only at high elevations, suggesting that the current warming trend is restricting its original distribution (Jacobson et al., 2018). Given their preference for cold habitats, the range and population densities of many bumblebees in Europe and North America appear to be restricted by global warming.

### 3.2.2. Other wild bees

Wild bees are estimated to provide at least 20% of pollination services in agricultural production (Losey and Vaughan, 2006). Their populations are largely dependent on food specialisation within a limited foraging range and habitat resources for nesting (Roulston and Goodell, 2011). Thus, 34% of the 105 bee species near Krakow (Poland) are rare and prefer wet meadows to other grasslands (Moron et al., 2008).

Using historical records on a grid of 10 km squares, declines in 52% of wild bee species in Britain and 67% in the Netherlands were observed after 1980, whereas increases in species richness were only observed in 10% of British cells and 4% of the Netherlands cells. Declining species were habitat and dietary specialists, univoltine and sedentary species in all cases, among which solitary bees were the most affected; moreover, plant species reliant on bee pollination alone were declining in both countries (Biesmeijer et al., 2006).

In Europe, an assessment of 1965 species of wild and naturalised bees found that 77 species are threatened and seven are critically endangered, including three endemic species: *Ammobates dusmeti*, *Andrena labiatula* and *Nomada sicilensis*. However, since population trends for 57% of species are unknown, 9.2% species of European bees were estimated to be declining (Nieto et al., 2014). An exhaustive analysis of almost half a million historical records of flower-visiting Hymenoptera in Britain since the mid-1800s, led to distinguish 4 main phases of extinction in that country: i) the second half of the 19th century, with the introduction of guano fertilisers and conversion of arable crops to permanent grasslands, which reduced floral resources; ii) after the First World War, when florally-diverse crop rotations were replaced with chemical fertilisers; iii) between 1930 and 1960, when most species went extinct probably due to changes in agricultural policy (i.e. Green Revolution) that fostered agricultural intensification; and iv) from 1987 to 1994, when rates of decline slowed down perhaps because the most sensitive species were already lost or reduced substantially (Ollerton et al., 2014). As agriculture occupies 70% of land-use in Britain, a causal relationship between species decline and farm management may involve multiple factors, including habitat changes and the use of chemical fertilisers and pesticides. The net result is the country-wide extinction of 23 species of flower-visiting Hymenoptera, including once common species.

The first long-term study on the distribution of wild bees in North America was done at Carlinville, Illinois (USA). A 1970–1972 survey found 140 bee species, implying a 32% reduction in biodiversity compared to historical records from the same location 75 years earlier: only 59 of the 73 prairie-inhabiting bees and 15 of the 27 forest-dwelling ones were recovered (Marlin and LaBerge, 2001). In addition to obvious changes in land use over the period, the authors blamed herbicide sprays that killed trees and vegetation that support specialist bees. Another comprehensive long-term study focused on stingless bees (Megachilidae) at Itasca State Park (Minnesota), where 293 species were found in eight habitats over 2010–2012. A comparison of the abundance of a subset of 30 species with historical records from 1937 showed that 11 species had declined in numbers, another 11 were missing while 4four new species had been found (Gardner and Spivak, 2014). In particular, *Megachile latimanus* had disappeared and no causal factors could be identified for its demise or for the sharp reductions in abundance of other species. A model that includes nesting resources and foraging landscapes as predictors of local bee densities suggests that wild bee abundance is high in resource-rich areas of the USA such as chaparral and desert shrublands, whereas intermediate densities are typical in temperate forests and grasslands, and low densities in agricultural crops (Koh et al., 2016). Wild bees were declining in 23% of the country between 2008 and 2013, mainly in the Midwest, Great Plains and the Mississippi valley, where grain production – particularly corn for biofuel production (Bennett and Isaacs, 2014) – had almost doubled during that period. Increased abundances were reported on a mere 10% of the land, specifically where crop fields had been abandoned or converted to shrublands. A detailed analysis of the interactions between 109 pollinating bees and their host plants was studied in 26 forests of Illinois (USA), and compared to historical records for the same site from the late 1800s and early 1970s. This floral network revealed many changes over the years, with only 24% of the original pollinator-plant interactions remaining. Shifts in network structure were due to losses of individual bee species in 45% of cases (Burkle et al., 2013). Overall, the network became less nested, more vulnerable, had lower redundancy and, while species richness per plant did not change much, experienced marked drops in abundance of pollinators over the past 40 years. Losses were more prevalent among specialist species, parasitic and cavity-nesters (e.g. Megachilidae), as predicted by other authors (Williams et al., 2010).

Losses of biodiversity among wild bees are also documented for tropical regions. A 12-year comparison of 24 orchid bees (Apidae: Euglossina) in two Atlantic forest reserves of Brazil showed declines in abundance of 63% species, mostly forest-dependent bees, while those of open and disturbed habitats increased in numbers (Nemesio, 2013). Similarly, regular surveys of wild bees visiting dry forest trees along a highway in Costa Rica over 1972–2004 showed a 60% decline in species up to 1996, coinciding with the urban sprawl in the region during that period (Frankie et al., 2009). Concurrently, populations of three species increased, probably due to more diversity of garden flowers in new dwellings. Bees belonging to the Halictidae and Megachilidae families suffered the greatest losses.

### 3.2.3. Honey bees (*Apis mellifera L.*)

In the USA, a peak of six million honey bee colonies was recorded in 1947 but this number has been declining ever since, with losses of 3.5 million over the past six decades at 0.9% annual rate of decline (Ellis, 2012). The demise started immediately after the introduction of the organochloride insecticide DDT in agriculture and has since continued unabated (Ellis et al., 2010). The main factors responsible for this steady decline include: widespread parasite and pathogen infections that are becoming more virulent in recent years (Anderson et al., 2011; Yang and Cox-Foster, 2007); lack of genetic variability; stress due to seasonal movement of hives for pollinating fruit and vegetable crops

(Smart et al., 2016); toxic pesticide residues found in the pollen and nectar or applied to hives for controlling *Varroa* mites (Johnson et al., 2013); poor nutritional value of agro-landscapes dominated by monocultures (e.g. corn, oilseed rape, cotton (Huang, 2012)); and finally the harsher climatic conditions of recent decades. The most likely explanation for the declines, however, is a combined effect derived from synergistic interactions between parasites, pathogens, toxins and other stressors (Alburaki et al., 2018; Goulson et al., 2015; Sánchez-Bayo et al., 2016b), which has resulted in the colony collapse disorder (CCD) (Underwood and vanEngelsdorp, 2007). Two thirds of American beekeepers presently lose about 40% of their colonies every year (Kulhanek et al., 2017), whereas 30% annual losses are reported for Europe, 29% in South Africa (Pirk et al., 2014) and 3–13% in China for both *A. mellifera* and *A. cerana* (Chen et al., 2017).

Managed colonies of honey bees worldwide are suffering from the same maladies and declining at similar rates (about 1% per year) in North America, Europe (Potts et al., 2010) and Australia (Gibbs, 2013). While parasites and diseases appear to be the proximate driver of the losses, synthetic pesticides have been involved in the losses from the very beginning (Ellis, 2012). The new generation of systemic insecticides, particularly neonicotinoids and fipronil, impair the immune system of bees (Di Prisco et al., 2013; Vidau et al., 2011) so that colonies become more susceptible to *Varroa* infections (Alburaki et al., 2015) and more prone to die when infected with viral or other pathogens (Brandt et al., 2017). Apart from bringing about multiple sub-lethal effects that reduce the foraging ability of worker bees (Desneux et al., 2007; Tison et al., 2016), neonicotinoid and fipronil insecticides equally impair the reproductive performance of queens and drones (Kairo et al., 2017; Williams et al., 2015), thus compromising the long-term viability of entire colonies (Pettis et al., 2016; Wu-Smart and Spivak, 2016).

#### 3.2.4. Cuckoo wasps (Chrysididae)

This rare group of parasitic wasps has recently been studied in Finland, and surveys reveal that 23% of the 48 local species are declining, together with one of the host species (Paukkunen et al., 2018). Unlike with other taxa, none of the cuckoo wasps seem to be increasing in numbers or distribution. Declining species are typically small, rare and tend to nest above ground, whereas populations of the larger and/or ground-nesting species appear to be stable. Authors attribute the declines to habitat loss (i.e. deforestation) for agricultural purposes, which restrict the availability of logs for nesting.

#### 3.2.5. Formicidae

Studies on ant (Formicidae) populations and trends are lacking except for a few invasive species (Cooling and Hoffmann, 2015; Vogel et al., 2010). Tropical deforestation has been invoked as a major cause for biodiversity losses of ants and other insects at the global scale – specifically for forest-inhabiting species (Wilson, 2002). Equally, logging of Nordic forests using established management practices was harmful to populations of the polydomous wood ant *Formica aquilonia*, because ants had their feeding and nesting resources restricted while abiotic conditions necessary for the development of the colonies had changed (Sorvari and Hakkarainen, 2007). Nothing is known about the fate of the multiple ant species that inhabit other types of habitats in both temperate and tropical settings.

### 3.3. Diptera

Hoverflies (Syrphidae) are important pollinators and key natural enemies of agricultural pests such as aphids, with a preference for damp habitats. Several surveys in Mediterranean countries have shown large local variations in biodiversity within this taxon, with 249 species alone in Greece (Petanidou et al., 2011) and 429 in Spain (Stefanescu et al., 2018). However, the only long-term study to date found parallel reductions in species richness among hoverflies in the Netherlands and the U.K. (Biesmeijer et al., 2006). That migratory hoverflies fared better than their sedentary counterparts in the latter two countries suggests that mobility is an important trait for survival. While plant species reliant on bee pollination alone were declining in both countries, plants pollinated by both bees and hoverflies were increasing only in the Netherlands.

### 3.4. Coleoptera

The largest order of insects includes important groups of predatory and saprophytic species that provide essential ecosystem services in pest control and recycling of organic matter among others.

#### 3.4.1. Carabidae

Ground beetles are a ubiquitous taxa and tiger beetles (Cicindelidae) are regularly used as indicators of biodiversity; this group occurs within habitats that harbour a diverse array of native butterflies and birds (Pearson and Cassola, 1992). Most of the changes among European carabids can be explained by habitat destruction, increased eutrophication due to agricultural intensification and expanding urbanisation. A study on 419 species within 10-km grid cells throughout the Netherlands, Belgium, Luxemburg and Denmark found that 34% of carabids declined between 1950 and 1980, with over 50% of xerophilic species of the genera *Amara*, *Harpalus* and *Cymindis* as well as *Carabus* decreasing in numbers (Desender and Turin, 1989). In the Netherlands, carabids with limited degrees of dispersal were the most affected, whereas those with large mobility or associated with man-made habitats had stable populations (Turin and den Boer, 1988).

In the U.K., dramatic declines of 49 out of the 68 carabids studied at 11 sites over 15 years, led to consider 26 species as vulnerable and eight endangered, whereas 19 species appear to be either stable or even increasing. Overall, a 16% loss of carabid beetle biomass was recorded during the 15-year period (Brooks et al., 2012). Changes in biodiversity were not linear and correlated with habitat and geographical variation, being most pronounced in mountainous regions of the west and north (64% of declining species), followed by moorlands (31%) and pastures (28%), whereas increases occurred in the southern downlands. Carabids in upland pastures, woodlands and hedgerows remained stable during the study period. Small species or those with spring breeding, dispersive or diurnal habits tend to be negatively affected. Microclimatic changes that alter soil moisture also affected some upland species (Brooks et al., 2012).

In New Zealand, 12 species of large carabid beetles are endangered and another 36 declining, together comprising about 8% of all known species in that country. Affected species belong mostly to two genera of giant carabids, *Mecodema* and *Megadromus* (McGuinness, 2007). The proportion of endangered carabids (about 4%) is twice as much as that of other local beetles, perhaps because they are large terrestrial species vulnerable to predation by introduced rats, hedgehogs, ferrets, weasels and possums. Habitat change due to forest clearance and conversion to pastures for sheep grazing have exacerbated the plight of these giant beetles, 92% of which are endemic and evolved in isolation during the past 80 million years.

#### 3.4.2. Coccinellidae

Harmon et al. (2007) reviewed 62 historical datasets of aphidophagous coccinellids in the USA and Canada, spanning 1914–2004. Although biased towards predatory species within agricultural landscapes, the surveys showed that ladybird species richness and population sizes did not change much until 1986, when a major decline in native species began to be noticed and affected 68% of species over the following 20 years (Harmon et al., 2007). At least two previously common species (i.e. *Adalia bipunctata* and *Coccinella novemnotata*) have since become very rare or entirely disappeared from the north-eastern USA (Wheeler, 1995). At the same time, 22 introduced species have been recorded, though only six of those have established in North

America. Two likely causes of the declines include: i) habitat change, either towards intensive agriculture in the Midwest States or through afforestation (i.e., New York State); and ii) competitive displacement by foreign generalist species such as *C. septempunctata* and *Harmonia axyridis* (Brown and Miller, 1998), possibly fuelled by a steep population build-up of invasive aphid pests in agricultural crops. *H. axyridis* is outcompeting native ladybirds in Great Britain (Roy and Brown, 2015), other European countries (Camacho-Cervantes et al., 2017) and Japan (Sato and Dixon, 2004), and gaining a competitive edge through its predation of aphids in agricultural crops (Rutledge et al., 2004).

Systematic records of abundance and distribution of ladybirds since 1976 in cereal crops, herbaceous plants and trees are available for the Czech Republic. Of the 13 species studied, six had declined in abundance while seven had increased, including *H. axyridis* (Honek et al., 2014). Agricultural intensification is the main driver of population changes in cereal crops and herbaceous stands, whereas coccinellid diversity and abundance in tree habitats remained stable over the 35-year period. Specifically, the extensive use of insecticides impacts both aphid pests and associated ladybird predators, and the recent conversion of crops to oilseed rape monocultures had an overall negative effect on *C. septempunctata* populations. Warming climate, by contrast, favoured the expansion of *Hippodamia variegata* (Brown and Roy, 2015).

In Britain, records of nine ladybird species collected by citizen scientists, along with systematic surveying between 1990 and 2013 were analysed by Brown and Roy, 2015). Five species were declining, two remained stable and two were expanding – *H. variegata* and *H. axyridis*. Changes in certain agricultural practices that led to lower aphid numbers in crops (i.e., reduced fertiliser use) may have resulted in the decline of three common native species (*A. bipunctata*, *C. undecimpunctata* and *Propylea quattuordecimpunctata*) and the concurrent increase of *H. variegata* and *H. axyridis*, indicating parallel coccinellid population trends for both the U.K. and continental Europe (Honek et al., 2014).

#### 3.4.3. Dung beetles

Dung beetles comprise three main groups: rollers (Scarabaeinae), tunnellers (Geotrupidae and most Scarabaeidae) and dwellers (Aphodiidae). Their unique ecological function is of vital importance to the livestock sector and for the soil fertility of grasslands. Studies on the decline of these specialized beetles are available only for the Mediterranean region, which has the largest diversity of dung beetles in Europe.

Roller dung beetles comprise a fifth of the 55 local species in Spain. An analysis of their abundance and distribution during the 20th century showed that while most species increased in numbers up to 1950, the relative abundance of nine of them dropped since then from 28% to 7%, while their distributional range contracted from 48% to 29% of the 10-km grid cells (Lobo, 2001). The most threatened species were *Scarabaeus pius* and *Gymnopleurus mopsus*, whereas populations of *S. cicatricosus* increased in its restricted southern area of distribution and those of *S. typhon* remained unchanged. Multivariate analyses reveal that large-scale urbanisation of the coasts for tourism and post-1950s agricultural intensification are primary causal factors.

In Italy, analysis of the abundance and distribution of 6870 records of 11 species of roller dung beetles for the entire 20th century showed a 31% reduction in both abundance and distribution affecting nine species (Carpaneto et al., 2007). Major declines started in the 1960s (2 species), increased in the 1970s (3 species) and became widespread in the 1980s (6 species). Their distribution, however, increased during the first half of the century and then decreased by 23% on a national level. The declines correlate with the local reduction of rangelands: 43% conversion of pastures to either forests or intensive agriculture since 1960. In addition, a shift from free-ranging livestock to stalled animals meant that dung was no longer available to foraging beetles. Two *Scarabaeus* and four *Gymnopleurus* species are considered threatened, and *G. mopsus* is probably extinct. The largest beetles are most at risk, suggesting that lower fecundity and enhanced predation by crows may be factors at play. The use of helminthicides (i.e. avermectins) and other anti-parasitic insecticides was considered of minor importance, though other authors have documented their negative impacts on dung beetles (Lumaret et al., 1993; Strong, 1992).

In France, a 1996 survey in the coastal region of the Camargue collected 337 individuals of 11 species only (nine Scarabaeidae and two Aphodiidae; none Geotrupidae), though the entire dung beetle fauna of the region is known to comprise 72 species (Lumaret, 1990). Such a significant drop in biodiversity affects more generalist species with greater dispersal abilities than the dwellers and rollers. Among the latter group, abundance of *Scarabaeus semipunctatus* has lowered 45-fold over 24 years, while populations of *S. sacer* are restricted to two sites between France and Spain (Lobo et al., 2001). The use of insecticides for mosquito control and livestock treatment as well as urbanisation are the main factors explaining the declines, since no agricultural changes have taken place in the area for decades.

#### 3.4.4. Saproxylic beetles

Saprophytic beetles play a major role in decomposition of wood in ecosystems, thus recycling nutrients that would otherwise be locked in decay logs and branches. Some species are also involved in pollination (Stefanescu et al., 2018).

In Europe, logging, wood harvesting and agricultural expansion have caused losses of old native forests, thus threatening the survival of 56 species of saproxylic beetles (a third of them endemic). While populations of at least 61 species are declining or have experienced a more confined distribution, nine others are increasing in numbers. Most threatened species are in Central and Eastern Mediterranean regions, and two endemic species, *Glaphyra bassetti* (Cerambycinae) and *Propomacrus cypriacus* (Euchiridae), are now regarded as critically endangered. However, since population trends for 57% of the 436 known species are unknown, the number of declining species could be even higher (Nieto and Alexander, 2010). The only long-term study available is for long-horn beetles (Cerambycidae) in Sweden, where 118 species are known from historical records. About half of the beetles had maintained the same distribution and relative abundance since the early 1900s (Lindhe et al., 2011). The status of the remaining 50% is affected by a local shift from agriculture to industrial, large-scale forestry: 26 species experienced significant declines, 32 increased in abundance, and 5–10 species are presumed extinct.

### 3.5. Hemiptera

One study of planthoppers and leafhoppers (Auchenorrhyncha) in protected grasslands of Germany was found (Schuch et al., 2012). These are typical phytophagous insects of open areas, accounting for a large proportion of the biomass of flying insects in natural and anthropogenic grasslands of Europe (Biedermann et al., 2005). Historical sweep-net samples (1963–1967) were compared to recent samples (2008–2010) at the same sites with respect to species diversity, species composition, and abundance. Regardless of the strong inter-annual variability in abundance and weather conditions, overall species richness did not change. However, species composition changed considerably, with 14 species declining (mostly specialists) and nine others increasing (mostly generalists), while one species (*Zyginidia scutellaris*) characteristic of acidic grasslands became very dominant. Moreover, median abundance decreased by 66% (from 679 to 231 individuals per site) over the 47-year period (Schuch et al., 2012). Airborne and soil acidification, partly due to agricultural intensification, is the main factor affecting local grassland composition and the associated herbivore fauna.

### 3.6. Orthoptera

A single long-term study on grasshoppers and crickets is available, conducted at the same German sites as above (Schuch et al., 2011). Their biodiversity in protected grasslands did not change over four

decades (median 9 species per site), and changes in species assemblages were small. The only significant change included a sharp decline in a grasshopper of bare soils (*Myrmeleotettix maculatus*) and increases in two generalist species of bush-crickets typical of open woodland and scrub (*Tettigonia viridissima*, *Phaneroptera falcata*). Contrasting with other taxa, few Orthoptera species showed detectable temporal trends, perhaps because most species are highly-adaptable polyphagous grazers. Nevertheless, about half of the species are considered threatened in Germany.

### 3.7. Odonata

Dragonflies (Anisoptera) and damselflies (Zygoptera) comprise a relatively small order of insects that depend on water bodies for their larval development. Both nymphs and imagos are predators of aquatic organisms and flying insects respectively, and they play an important role in controlling nuisance mosquitoes and agricultural pests, e.g. of rice (Painter et al., 1996; Relyea and Hoverman, 2008). Of the 118 aquatic species of endangered insects listed by the IUCN, 106 are Odonata (Kalkman et al., 2010), although it is clear that other aquatic taxa are underrepresented due to insufficient knowledge (DeWalt et al., 2005). A recent IUCN assessment indicates that 10% of the world's Odonata are threatened with extinction, although that study only covered a quarter of all species known and acknowledged data gaps for 35% of species, particularly those from tropical and Australasian regions (Clausnitzer et al., 2009). Given the above, 15% of all species may be threatened.

In the USA, recent surveys at 45 sites across California and Nevada were compared to historical records from 1914 to 1915. Occurrence rates of 52 species of dragonflies and damselflies (65% of all recorded) have declined over the 98-year period while those of 29 species have increased. Two generalist and pollution-tolerant species that were not recorded in 1914–1915 greatly expanded their range into California and became common, particularly in urban areas. At least nine species declined significantly, including four species (*Sympetrum danae*, *S. costiferum*, *Ophiogomphus occidentis* and *Libellula nodisticta*) that were also rare in early surveys. Declines occurred mostly among habitat specialists, whereas increases were recorded for generalist and migratory species that replaced the losses at the same sites. Specialist species included those with overwintering diapause, which appear to have declined due to an increase of minimum temperature over the period (Ball-Damerow et al., 2014). While species richness has not declined, Odonata assemblages have become more homogeneous in species composition, which is typically an effect of urbanisation (McKinney, 2006).

In Europe, 15% of the 138 Odonata species are currently threatened, with two damselflies (*Ceriagrion georgifreyi* and *Pyrrhosoma elisabethae*) and one dragonfly (*Cordulegaster helladica* sp. *kastalia*) critically endangered in the Balkan Peninsula. A quarter of all species (33) are declining in population numbers and distribution, whereas 10% of them are increasing and about half remain stable. Major declines took place during post-1960 agricultural intensification, with canalisation of rivers for irrigation and water pollution by urban runoff, pesticides and fertilisers (i.e. eutrophication) being the main drivers of population extinctions over large areas (Kalkman et al., 2010). Ubiquitous species such as *Coenagrion puella* and *Sympetrum striolatum*, however, increased and shifted their range some 300 km northwards in Britain between 1960 and 1970 and 1985–1995 (Hickling et al., 2005). In central Finland, populations of 20 common species of Zygoptera and Anisoptera were surveyed at 34 small creeks over 1995–1996, and their distribution patterns were compared with historic records from 1930 to 1975. Two specialist and lentic dragonflies, *Coenagrion johanssoni* and *Aeshna caerulea* have disappeared from streams, and 45% of the 219 surveyed populations vanished. Local extinctions occurred in peat bogs and dynamic waters upstream, which are habitats for lentic-specialist species, whereas downstream water bodies had lower losses. Generalist species (i.e., those that breed in both lentic and lotic waters) were less likely to become locally extinct. The construction of agricultural ditches and habitat fragmentation from forestry further impacted on populations of rare species (Korkeamäki and Suhonen, 2002).

In Japan, 57 out of 200 Odonata species are declining, with 23 being vulnerable and 19 endangered (Kadoya et al., 2009). The largest drops in abundance and distribution are among lentic species once common in rice paddy fields (e.g., *Lestes japonicus*, *Libellula angelina*, *Sympetrum maculatum* and S. *uniforme*). Island endemics are next in the extinction list, whereas those of lotic habitats of mountain streams are the least affected. The sharp decline in populations of red dragonflies (*Sympetrum* spp.) since the mid-1990s (Fukui, 2012; Futahashi, 2012) has been linked to the use of fipronil and neonicotinoid insecticides (Nakanishi et al., 2018), which affect the aquatic nymphal stages by curtailing the emergence of adults (Jinguji et al., 2013).

Of the 155 Odonata species recorded in South Africa, 13 are declining and four are extinct (Samways, 1999). The protection of rare species in nature reserves of that country does not necessarily guarantee their survival, as current livestock management and other human activities negatively impact on these aquatic insects.

### 3.8. Other freshwater taxa

Freshwater insect taxa tend to have rather inflexible life cycles, with many species being univoltine, thus making them particularly sensitive to habitat change. Flow alterations, habitat fragmentation, pollution and invasive species are the main threats to all aquatic organisms, including insects (Allan and Flecker, 1993; Zwick, 1992). Data pertaining to three main orders of freshwater insects, Plecoptera, Ephemeroptera and Trichoptera, are reported here but no surveys were found for Coleoptera (e.g. Dytiscidae, Hydrophilidae), Hemiptera (e.g. Notonectidae, Gerridae) or Diptera (e.g. Chironomidae, Tipulidae).

#### 3.8.1. Plecoptera

Stoneflies (Plecoptera) are numerically and ecologically a significant component of the entomofauna of running waters, typified by high degrees of endemism and narrow ecological requirements (Zwick, 2000). More than half of the species are univoltine and their nymphs require mainly cold and well-oxygenated waters of temperate and cold regions. In Europe, once common species of lowland rivers such as *Taeniopteryx araneoides* and *Oemopteryx loewi* are now extinct over the entire continent, while *Isogenus nubecula* has locally disappeared (Fochetti and de Figueroa, 2006). The percentage of species threatened with extinction ranges from 50% in Switzerland (Aubert, 1984) to 13–16% in Mediterranean countries like Spain and Italy, where many species are endemic. Up to 63% of the 516 European species of stoneflies are susceptible to climate change, particularly species endemic to the high mountains of the Alps, Pyrenees and Mediterranean peninsulas, which experience altitudinal shifts in habitat (Tierno de Figueroa et al., 2010). Although stoneflies are relatively tolerant of acidification as compared to other macro-invertebrates, they are highly sensitive to changes in water flows and eutrophication by organic pollution (Tixier and Guérold, 2005).

In the Czech Republic, species diversity and abundance of 78 stoneflies in rivers, streams and lakes were compared at 170 sites between 1955 and 1960 and 2006–2010 (Bojková et al., 2012). Three quarters of the changes in species diversity occurred at low- and mid-altitude streams, with pollution, impoundment and channelization affecting those sites. Lowland river habitats had five threatened species of the original 14 species recorded at the turn of the 19th century, while four are now extinct. Over a 50-year time frame, 12% of the species were no longer found, whereas two new species have appeared (*Brachyptera monilicornis* and *Leuctra geniculata*). Moreover, 22% species had declined by > 50%, including once common species such as *Perla abdominalis*, *Amphinemura standfussi* and *Nemurella pictetii*, and a further 10% have become vulnerable. Contrary to terrestrial taxa, most

declines were observed among habitat generalists and less specialized species (60–70%), which are tolerant to organic pollution. These species survived a first wave of extinctions during the 1920s–1930s and the industrialisation of the 1960s–1980s. Sites affected by organic pollution showed, however, the greatest change in community assemblage, particularly in agricultural and urbanised settings, whereas communities in montane and sub-montane areas have remained almost intact: only 17–33% of sensitive and eurytopic species declined since the mid-1990s (Bojková et al., 2014); some degree of species recovery has been observed following pollution mitigation in acidified habitats (Nedbalová et al., 2006). In Switzerland, half of the species of stoneflies and mayflies in water courses of industrial and agricultural areas were lost between 1940s and 1980s (Küry, 1997), and the same occurred in other European countries and the USA, where the entire Plecoptera fauna of lowland rives can now be considered threatened.

In Illinois (USA), 29% of the 77 local stonefly species were lost and 62% of the remainder became threatened over the past century (DeWalt et al., 2005). Main losses occurred in the large rivers and agricultural areas of the Grand Prairie during the 1940s and 1950s, when both agricultural and urban expansion took place. Structural modification of river flows due to dams, channels and tile drainage networks have all impacted negatively on these insects, as they increased siltation and organic waste. The large, long-lived species of Perlidae (summer stones) and Perlodidae (spring stones) were impacted the most, and 36% of summer stones have gone extinct since 1860. For sensitive genera such as *Acroneuria*, 88% of the entire contingent was lost over the past century, whereas genera tolerant to organic pollution such as *Perlesta* have increased 4-fold. Species losses were largest within semi-voltine and univoltine stoneflies adapted to permanent waters.

#### 3.8.2. Ephemeroptera

The most comprehensive checklist of mayflies (Ephemeroptera) of the Czech Republic recognised 107 species of which four had become extinct, seven are critically endangered, seven endangered, 16 vulnerable and 14 near threatened – a 43% overall decline of local species of mayflies (Zahrádková et al., 2009). A comparison of local mayfly communities in 60 streams between 1955 and 2011 showed clear changes in species composition but no losses in biodiversity except for the large lowland rivers, which lost five specialist species but gained several silt-tolerant species (Zedková et al., 2015). Biodiversity, however, increased slightly in mid- and upper streams and rivers, indicating perhaps some recovery given the substantial reduction in water pollution post-1989 (Bojková et al., 2014). Two species became extinct (*Isonychia ignota* and *Ephemerella mesoleuca*), three became very rare, 11 were declining and nine were expanding their range, including the dominant *Centroptilum luteolum* and *Baetis niger*. Main changes were due to losses or turnover of previously common and widespread species such as *B. alpinus* and *Epeorus assimilis*, so the overall dissimilarity among sites (15–30%) was mainly driven by species replacement. The current communities have shifted towards more simplified and less specialized assemblages in large rivers, whereas mayflies in small creeks have been replaced with species tolerant to pollution and siltation.

In North America, a total of 672 species of mayflies are listed though no details are available regarding distribution or status (McCafferty et al., 2010; McCafferty, 1996). A similar compilation for North and South Carolina (USA) reported 204 species (Pescador et al., 1999), but again no status was indicated. A later study in relation to 10 rare species revealed, however, that four of the species collected in the early 20th century should be considered extinct (McCafferty, 2001).

#### 3.8.3. Trichoptera

Another taxon of inconspicuous insects, the caddisflies (Trichoptera) has been poorly studied. Of the 278 species recorded in relatively undisturbed regions of Minnesota (USA) since the 1890s, 6–37% of species losses have occurred in different areas, especially within the Limnephilidae (44% of species), Phryganeidae (21%) and Leptoceridae (12%) families (Houghton and Holzenthal, 2010). *Agrypnia glacialis* and *Anabolia sordida* are currently extinct, and 17 rare species have not been found since the 1950s, while only one record is known of *Limnephilus secludens* since 1985 (Houghton and Holzenthal, 2010). All species in the affected families are either univoltine or semivoltine and, because of their long lifespan and feeding habits, are particularly vulnerable to anthropogenic disturbances in water courses. The majority of losses are found among shredder (72%) and predatory species (11%), in agreement with loses of aquatic taxa in other countries (Jenderedjian et al., 2012; Karatayev et al., 2009). The regional caddisfly community is now dominated by filtering collectors (65% of species), with tolerant species such as *Potamyia flava* (Hydropsychidae) having increased in abundance several-fold since the 1950s, particularly in large rivers and agricultural regions that now account for over 95% of the original prairie habitats.

## 4. Discussion

Biodiversity loss has become a major global issue, and the current rates of species decline – which could progress into extinction – are unprecedented (Barnosky et al., 2011; Pimm and Raven, 2000). Yet, until recently, most scientific and public attention has focused on charismatic vertebrates, particularly on mammals and birds (Ceballos and Ehrlich, 2002; Manne et al., 1999), whereas insects were routinely underrepresented in biodiversity and conservation studies in spite of their paramount importance to the overall functioning and stability of ecosystems worldwide (Fox, 2013; McKinney, 1999; Thomas et al., 2004).

This review brings to the fore the demise of major insect taxa (albeit no studies are available for most Diptera, Orthoptera and Hemiptera), which started at the dawn of the 20th century, accelerated during the 1950s–1960s, and attained alarming proportions globally over the last two decades. Our aim is to draw attention to the extent of the problem and point out its drivers, so that adequate conservation measures may be implemented and prioritised.

From our compilation of published scientific reports, we estimate the current proportion of insect species in decline (41%) to be twice as high as that of vertebrates, and the pace of local species extinction (10%) eight times higher, confirming previous findings (Dirzo et al., 2014). At present, about a third of all insect species are threatened with extinction in the countries studied (Table 1). Moreover, every year about 1% of all insect species are added to the list, with such biodiversity declines resulting in an annual 2.5% loss of biomass worldwide (Fig. 2).

Among terrestrial taxa, the largest losses of biodiversity are among dung beetles in Mediterranean countries, with > 60% of species in decline and a large proportion considered threatened (Fig. 3a). About half of Coleoptera and Lepidoptera species (both moths and butterflies) are declining at a faster rate than the annual average (2.1% and 1.8% respectively, Fig. 2). A similar trend is observed among bees, where one in six species have gone regionally extinct. The fate of other pollinators such as hoverflies is, however, largely unknown. In agreement with biodiversity losses reported in other animal taxa (Ricciardi and Rasmussen, 1999), declines are even higher among aquatic insects, despite the scarce knowledge available for most countries: 33% of aquatic insects are threatened compared to 28% among terrestrial taxa (Fig. 3b).

Insect declines appear to be similar in tropical and temperate regions of the world (mean 45.3% vs 45.4% of species, $p = 0.93$), though the low number of studies in the tropics ($n = 3$) does permit statistical comparison. Within temperate regions, the U.K. seems to have the largest documented declines across taxa (60% of species), followed by North America (51%) and Europe (44%), but with no significant differences among them ($p = 0.21$, $F = 3.15$, $df = 59$, ANOVA); within Europe, insect declines are also similar between Mediterranean and

**Table 1**
Proportion of declining and threatened species per taxa according to IUCN criteria (> 30% decline), the annual rate of decline in species (i.e. additional declines per year) and the local or regional extinction rate (i.e. percent of species not observed in > 50 years).

| Taxon | Declining (%) | Threatened (%) | Annual species declines (%) | Extinction rate (%) | No. Reports |
|---|---|---|---|---|---|
| A) Insects | 41 | 31 | 1.0 | 10 | 73[a] |
| Coleoptera | 49 | 34 | 2.1 | 6.6 | 12 |
| Diptera (Syrphidae) | 25 | 0.7[g] | n.a. | n.a. | 4 |
| Ephemeroptera | 37 | 27 | 0.6 | 2.7 | 3 |
| Hemiptera (Auchenorrhyncha) | 8[g] | n.a. | 0.2[g] | n.a. | 1 |
| Hymenoptera | 46 | 44 | 1.0 | 15 | 21 |
| Lepidoptera | 53 | 34 | 1.8 | 11 | 17 |
| Odonata | 37 | 13 | 1.0 | 6 | 6 |
| Orthoptera | 49 | n.a. | 1.0 | n.a. | 1 |
| Plecoptera | 35 | 29 | 0.6 | 19 | 7 |
| Trichoptera | 68 | 63 | 0.6 | 6.8 | 1 |
| Terrestrial | 38 | 28 | 1.2 | 11 | 56 |
| Aquatic | 44 | 33 | 0.7 | 9 | 17 |
| B) Vertebrates | 22 | 18 | 2.5 | 1.3 | 11 |
| Amphibians | 23 | 23 | n.a | n.a. | 1[b] |
| Birds | 26 | 13 | 2.3 | 0.8 | 3[c] |
| Mammals (land) | 15 | 15 | 0.1 | 1.8 | 3[d] |
| Mammals (Chiroptera) | 27 | n.a. | 5.2 | 1.2 | 3[e] |
| Reptiles | 19 | 19 | n.a. | n.a. | 1[f] |

[a] This paper; see Table S1.
[b] Temple and Cox, 2009.
[c] Thomas et al., 2004; Birdlife_International, 2015.
[d] Ceballos and Ehrlich, 2002; Temple and Cuttelod, 2008; Temple and Terry, 2009.
[e] Mickleburgh et al., 2002; Mitchell-Jones, 1990; Van der Meij et al., 2015.
[f] Cox and Temple, 2009.
[g] Insufficient data.

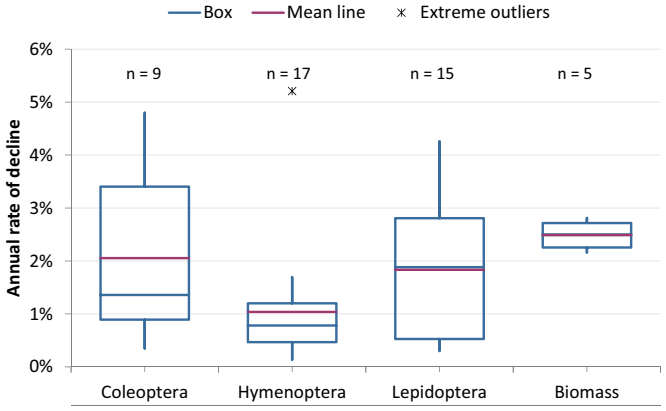


**Fig. 2.** Annual rate of decline of the three major taxa studied (percentage of species declining per year) and of insect biomass.

central or northern countries (p = 0.27, F = 4.15, df = 33, ANOVA). Studies from all other regions have a significantly lower proportion of insect declines (23%, p = 0.01, F = 2.51, df = 68, ANOVA), except for a single study that showed a 62.5% decline of orchid bees (Euglossina) in Brazil, which can be regarded as an outlier (Fig. 4).

The pace of modern insect extinctions surpasses that of vertebrates by a large margin, although the extent of losses cannot be accurately quantified. This is largely due to a dearth of historical knowledge in many regions (e.g. China, sub-tropical and tropical countries and Australia), an absence of comparative surveys for multiple insect orders and an underestimation of the host-associated species (e.g., specialist herbivores, pollinators, obligate parasitoids and parasites) that are lost through co-extinction of their host plant or animal (Dunn, 2005; Koh et al., 2004). Since the declines affect the majority of species in all taxa, it is evident that we are witnessing the largest extinction event on Earth since the late Permian and Cretaceous periods (Ceballos et al., 2017; Raup and Sepkoski Jr, 1986). Because insects constitute the world's most abundant and speciose animal group and provide critical services within ecosystems, such event cannot be ignored and should prompt decisive action to avert a catastrophic collapse of nature's ecosystems (May, 2010).

Most worrying is the fact that the declining terrestrial insect fauna comprise not only specialists with narrow ecological requirements, such as dependence on particular host plants (e.g., *Coenonympha oedippus* in bogs), ecological niches (e.g., roller dung-beetles) or restricted habitats (e.g., *Bombus terricola* in the USA), but also generalist species that were once common in many countries (e.g., *Aglais io* in the Netherlands or *Macaria wauaria* in the U.K.). This suggests that the causes of insect declines are not tied to particular habitats, but instead affect common traits shared among all insects (Gaston and Fuller, 2007). The disappearance of habitat generalists is particularly notorious among aquatic insects, for which major losses have been recorded among stoneflies, mayflies, caddisflies and dragonflies that once inhabited the large rivers of Europe and North America (Bojková et al., 2014). Thus, the biodiversity of the Rhine river plummeted during the industrial expansion of the 1930s, and subsequent efforts aimed at its recovery have failed to bring back many of the native species (Marten, 2001). Interestingly, aquatic insect communities remain stable or show lesser declines in pristine mountain streams and lakes. In aquatic environments, the evidence points to pollution as the main driver of the declines and extinctions recorded so far.

Anthropogenic pressure is shifting multiple insect communities towards species-poor assemblages dominated by generalists (White and Kerr, 2007), with current biodiversity losses and shifts in community composition being the forerunners of extinction (Chapin-III et al., 2000). In aquatic settings, the disappearance of susceptible species and their steady replacement with (often non-native) tolerant ones poses a major threat to freshwater biodiversity (Karatayev et al., 2009). Species losses are expected to lead to a steady decay of insect-mediated ecosystem services, which are likely to be provided by fewer and less specialized species (Bartomeus et al., 2014; Pimentel, 1961). As insect biodiversity is essential for the proper functioning of all ecosystems, the current trends are disrupting – to varying degree – the invaluable pollination, natural pest control, food resources, nutrient recycling and decomposition services that many insects provide (Aizen et al., 2009;

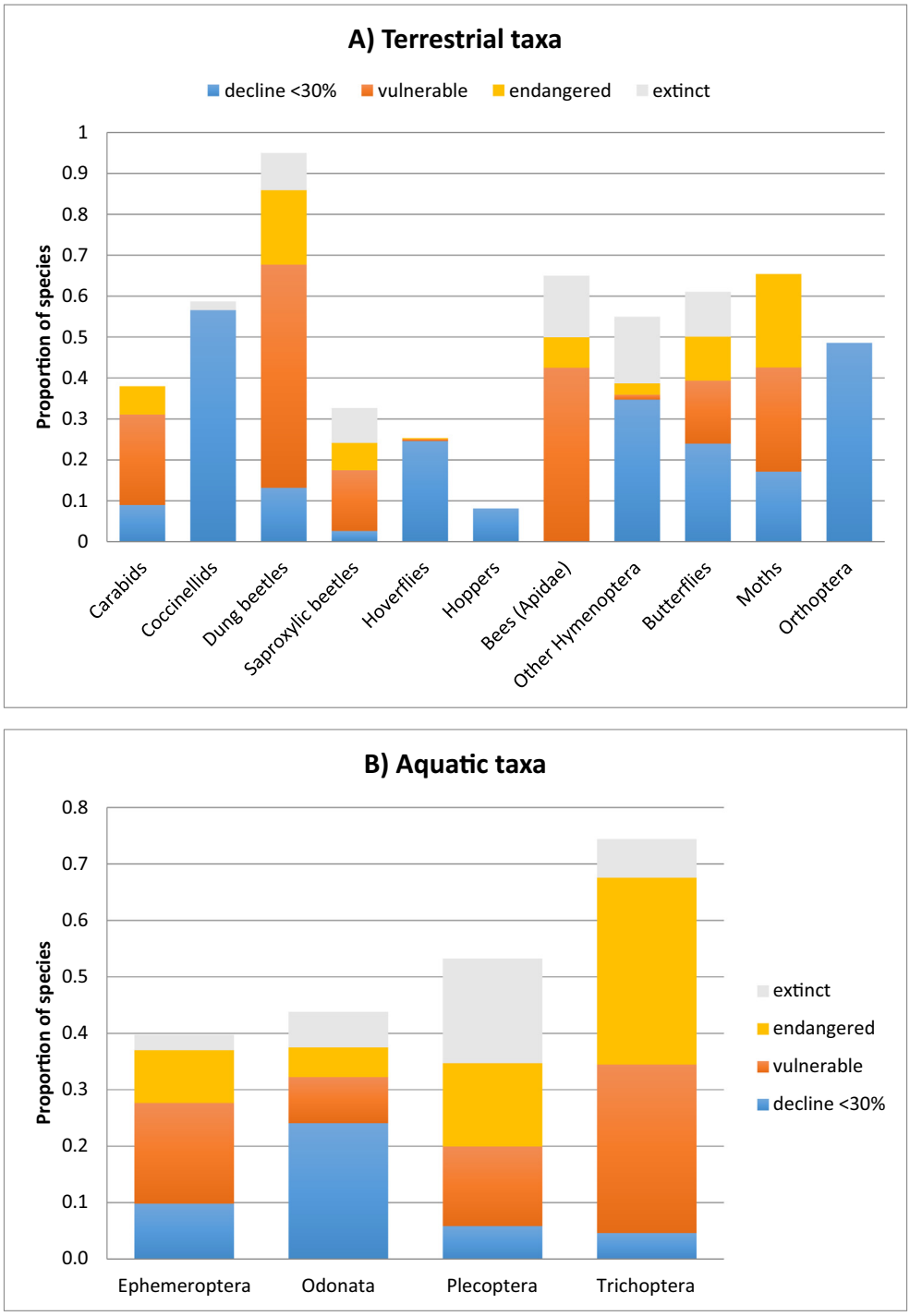


**Fig. 3.** Proportion of insect species in decline or locally extinct according to the IUCN criteria: vulnerable species (> 30% decline), endangered species (> 50% decline) and extinct (not recorded for > 50 years). A) terrestrial taxa; B) aquatic taxa.

Davis et al., 2004; Kreutzweiser et al., 2007).

While countless insect species are disappearing, few others are occupying vacant niches and expanding their distribution. In terrestrial ecosystems, most of the occupying species are generalists with diverse ecological preferences (e.g., *Bombus impatients*, *Plusia putnami*, *Laemostenus terricola* and *Hippodamia variegata*). In aquatic environments, species replacement is also mediated by ecological traits such as degree of tolerance to pollutants (e.g. *Sympetrum striolatum*, *Brachyptera risi* and *Potamyia flava*), with communities thus becoming more uniform and less diverse in composition (Houghton and Holzenthal, 2010). Species replacement may help retain the delivery of certain ecosystem services, but it's unclear to what extent natural ecosystems can sustain their overall ecological resilience (Memmott et al., 2004).

Species extinctions equally impact the overall biomass of entire ecosystems, as insects form the base that supports intricate food webs. Indeed, the essential role that insects play as food items of many vertebrates is often forgotten. Shrews, moles, hedgehogs, anteaters, lizards, amphibians, most bats, many birds and fish feed on insects or depend on them for rearing their offspring. Even if some declining insects might be replaced with others, it is difficult to envision how a net drop in overall insect biomass could be countered. The large declines in insect biomass observed in Europe (Hallmann et al., 2017) and Puerto Rico

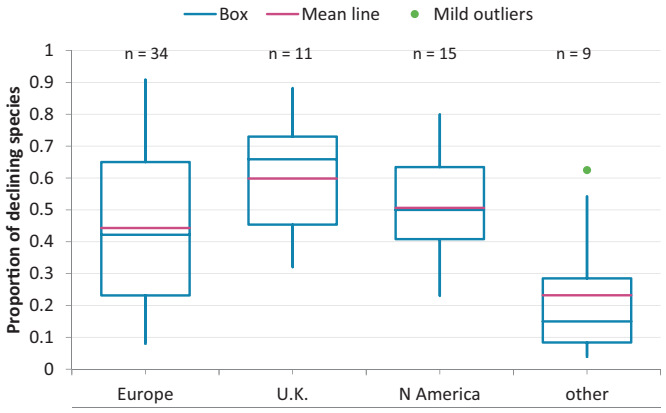


**Fig. 4.** Proportion of declining insect species in different regions of the world.

(Lister and Garcia, 2018) inevitably lead to a starvation of dependent vertebrates (Hallmann et al., 2014; Lister and Garcia, 2018; Poulin et al., 2010; Wickramasinghe et al., 2003). This kind of cascading effect was first observed with grey partridge (*Perdix perdix*) populations in England since 1952, and was ascribed to reproductive failure. The ultimate cause of the partridge collapse was a combined use of insecticides and herbicides in agricultural land, leading to insufficient insect numbers to feed the chicks (Potts, 1986). Equally, in the U.K. the diversity and abundance of bats in intensive agricultural landscapes is considerably lower than on organic farms because of a reduction in insect biomass caused by pesticide use in the former settings (Wickramasinghe et al., 2004), and direct insecticide exposure through the bats' prey items (Mispagel et al., 2004; Stahlschmidt and Bruhl, 2012).

### 4.1. Drivers of the declines

A large proportion of studies (49.7%) point to habitat change as the main driver of insect declines, a factor equally implicated in global bird and mammal declines (Chamberlain and Fuller, 2000; Diamond, 1989). Next on the list is pollution (25.8%) followed by a variety of biological factors (17.6%), whereas few studies (6.9%) indicate climate change as triggering the losses (Fig. 5; Table S2).

#### 4.1.1. Habitat change

Habitat change is an immediate consequence of human activities. Its global pace and scope has been expanding over the past centuries, with increasing amounts of land being transformed to provide dwellings, facilitate transportation and enable tourism (urbanisation), grow food

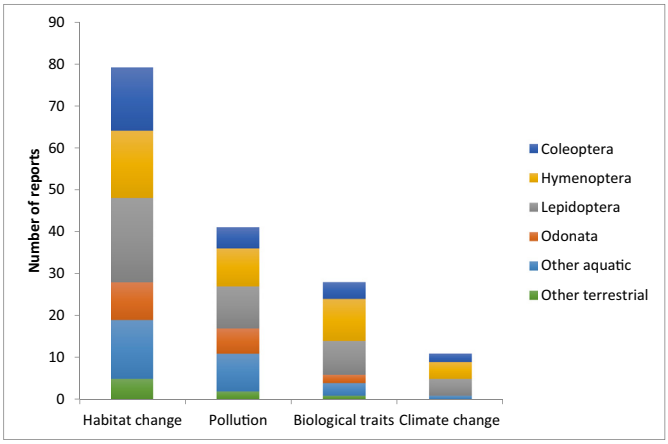


**Fig. 5.** The four major drivers of decline for each of the studied taxa according to reports in the literature.

(agriculture) and manufacture goods (industrialisation) at the expense of various natural habitats. Among Coleoptera, Lepidoptera and Hymenoptera, land-use change and landscape fragmentation is surely the main cause of species declines (Fig. 5), with agricultural conversion and intensification for food production listed in 24% of the reports (Fig. 6). Urbanisation, by contrast, is reported in 11% of cases, while deforestation appears in 9% of reports.

As agricultural crops comprise about 12% of the total land surface on the planet (FAO, 2015), farming directly affects a considerable proportion of insect species (Dudley and Alexander, 2017). In Europe and North America, the expansion of the agricultural frontier took place mostly in the first half of the 20th century, whereas in South America, Africa and Asia occurred mainly in the second half of the century (Foley et al., 2005; Gibbs et al., 2010). In its wake, rare species associated with pristine ecosystems and natural habitats either retreated or were entirely lost (Grixti et al., 2009; Ollerton et al., 2014). Major insect declines occurred, however, when agricultural practices shifted from traditional, low-input farming style to the intensive, industrial scale production brought about by the Green Revolution (Bambaradeniya and Amerasinghe, 2003; Ollerton et al., 2014). The latter practices did not necessarily involve deforestation or habitat modification (e.g., grassland conversion, drainage of wetlands) but rather entailed the planting of genetically-uniform monocultures, the recurrent use of synthetic fertilisers and pesticides, the removal of hedgerows and trees in order to facilitate mechanization, and the modification of surface waterways to improve irrigation and drainage. Monocultures led to a great simplification of insect biodiversity among pollinators, insect natural enemies and nutrient recyclers, and created the suitable conditions for agricultural pests to flourish. A quarter of the reports indicate these agriculture-related practices as the main driver of insect declines in both terrestrial and aquatic ecosystems (Wilcove et al., 1998).

The susceptibility of specialist pollinators to land-use changes (involving loss of floral resources, nesting and hibernation sites), appears to be a determining factor in the decline of many bumblebees and wild bees (Williams and Osborne, 2009). For specialist ground beetles, the loss of hedgerows and trees likely triggered their decline (Brooks et al., 2012). Declines in moths are tied to the fate of their overwintering larval host plants: forbs for species overwintering as larvae, and trees for those overwintering as egg, pupa, or adult. The combined removal of weeds and trees in intensive agricultural settings may thus explain the decline of moth species overwintering as larvae (Fox, 2013; Mattila et al., 2006; Merckx et al., 2009; Pocock and Jennings, 2008). Conversely, the change from intensive farming to organic farming has led to increases in abundance and diversity of moths (Taylor and Morecroft, 2009), while the abandonment of grazing land has allowed the recovery of some common butterflies (Kuussaari et al., 2007).

Agricultural intensification also entails stream channelization, draining of wetlands, modification of floodplains, and removal of riparian canopy cover with subsequent loss of soil and nutrients – all resulting in homogenization of stream microhabitats and alteration of aquatic insect communities (Houghton and Holzenthal, 2010). These activities increase eutrophication, siltation and sedimentation in water bodies, thus reducing the richness of shredders and predators while favouring filterer species (Burdon et al., 2013; Niyogi et al., 2007; Olson et al., 2016). Diverse communities of aquatic plants are an important habitat component in lentic systems such as paddy fields, allowing herbivory, oviposition and emergence of many insects and providing refugia for Odonata nymphs (Nakanishi et al., 2014). In general, loss of permanent flows in streams and rivers leads to a decrease of biodiversity (King et al., 2016), whereas irrigation and man-made water bodies in urbanised areas may have favoured certain species (Kalkman et al., 2010).

In recent decades, urbanisation has taken over agricultural land across the globe, causing the disappearance of many habitat specialists and their replacement with a few generalists adapted to the artificial

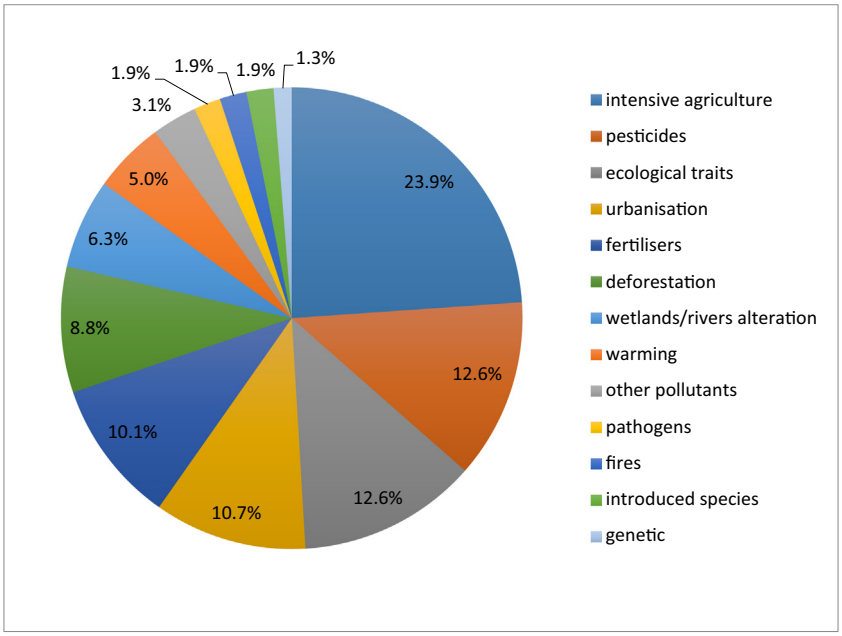


**Fig. 6.** Main factors associated with insect declines – see also Fig. 5.

human environment. However, such losses can be partially counterbalanced by the creation of urban parklands and gardens, which offer refuge to native and newly-colonising species, including pollinators like *Bombus* spp. (Botías et al., 2017) and butterflies like *Lycaena phlaeas* and *Aphantopus hyperantus* (van Dyck et al., 2009).

In tropical countries of South America, Africa and Asia, deforestation has been and still is a main driver of biodiversity loss and insect declines (Carrasco et al., 2017; Wilson, 2002), including dragonflies (Samways, 1999). Recent research on herbariums of Pacific islands suggests that deforestation and other human impacts on those ecosystems are not confined to the extinction of birds, mammals and snails (Kingsford et al., 2009) but also of insects such as leafminers (Lepidoptera: Gracillariidae) (Hembry, 2013). In Europe, deforestation is the main driver of saproxylic beetles' decline (Nieto and Alexander, 2010). Conversely, afforestation may increase the number of generalist butterflies by increasing habitat diversity at the forest edge (Kuussaari et al., 2007), but woodland diversity, structural and micro-climatic heterogeneity are far more important than forested area per se for maintaining the diversity of moths, butterflies as well as birds (Fuller et al., 2005; van Swaay et al., 2006). Very few generalist species benefit and expand under afforestation, and some European butterfly species even exhibited notable declines (van Swaay et al., 2006). In Britain, a 20-fold increase in conifer plantations since the 19th century did not increase biodiversity nor abundance of Lepidoptera species (Brereton et al., 2011; Fox, 2013).

#### 4.1.2. Pollution

Pollution is the second major driver of insect declines (Fig. 5). Sources of environmental pollution include fertilisers and synthetic pesticides used in agricultural production, sewage and landfill leachates from urbanised areas and industrial chemicals from factories and mining sites. Among these, pesticide pollution is reported in 13% of cases (Fig. 6), followed by fertiliser inputs (10%) and to a lesser extent urban and industrial pollutants (3%).

Intensive agriculture implies the systematic and widespread use of pesticides for controlling crop pests (insecticides), competing weeds (herbicides) and fungal infections (fungicides) among others (Dudley and Alexander, 2017). In terms of toxicity, insecticides are by far the most toxic to all insects and other arthropods, followed by fungicides but not herbicides (Mulé et al., 2017; Sánchez-Bayo and Goka, 2014). Herbicides, however, reduce the biodiversity of vegetation within the crops and in surrounding areas through drift (Egan et al., 2014) and runoff, thus impacting indirectly on the arthropod species that depend upon wild plants, which either disappear completely or decline significantly in numbers (Goulet and Masner, 2017; Marshall et al., 2003). Thus, the application of herbicides to cropland has had more negative impacts on both terrestrial and aquatic plants and insect biodiversity than any other agronomic practice (Hyvonen and Salonen, 2002; Lundgren et al., 2013). Pesticides have caused the decline of moths in rural areas of the U.K. (Hahn et al., 2015; Wickramasinghe et al., 2004) and pollinators in Italy (Brittain et al., 2010); broad-spectrum insecticides reduce the abundance and diversity of beneficial ground-dwelling and foliage-foraging insects (Lundgren et al., 2013); systemic insecticides reduce populations of ladybirds and butterflies in gardens and nurseries (Krischik et al., 2015), and inflict multiple lethal and sub-lethal effects on bees (see 3.2.3) and other arthropods. Fungicides are not less damaging to insects, and synergism of a particular group of compounds (i.e., azoles) with insecticide toxicity (Biddinger et al., 2013; Pilling and Jepson, 1993) is certainly involved in honey bee collapses (Simon-Delso et al., 2014).

Pyrethroid, neonicotinoid and fipronil insecticides have a devastating impact on aquatic insects and crustaceans due to their high acute and chronic toxicity (Beketov and Liess, 2008; Kasai et al., 2016; Mian and Mulla, 1992; Roessink et al., 2013), thus reducing significantly their abundance in water bodies (van Dijk et al., 2013). Persistent residues of fipronil in sediments inhibit the emergence of dragonflies (Jinguji et al., 2013; Ueda and Jinguji, 2013) and the development of chironomids and other insect larvae, with negative cascading effects on fish survival (Weston et al., 2015). Systemic insecticides impair the long-term viability of shredder larvae that decompose leaf litter and other organic material (Kreutzweiser et al., 2008), undermine the basis of the insect food web (Sánchez-Bayo et al., 2016a) and thus derail natural biological control mechanisms e.g., in rice paddy ecosystems (Settle et al., 1996). Also, these products readily translocate to pollen, nectar, guttation drops, and all tissues of the treated crops and adjacent plants, impacting on nectar-feeding biota such as bees, butterflies, hoverflies and parasitic wasps (van der Sluijs et al., 2015). Unlike the short-term effects of other pesticides on aquatic organisms (Schäfer et al., 2011; van den Brink et al., 1996), neonicotinoids do not allow the recovery of univoltine and semivoltine aquatic insects (Beketov et al.,

2008), and appear to be the main driver of dragonfly declines in Japan (Nakanishi et al., 2018).

Also, the treatment of livestock with persistent avermectins and insect growth regulators has inadvertently contributed to a reduction of dung beetles in many countries, as residues of these pesticides in dung pats eliminate the developing larvae (Lumaret et al., 1993; Strong, 1992; Wardhaugh and Mahon, 1991). Unfortunately, more tolerant species of Ceratopogonidae and Psychodidae flies that breed in the same pats had their numbers boosted in Japan (Iwasa et al., 2005).

Overall, the systematic, widespread and often superfluous use of pesticides in agricultural and pasture land over the past 60 years has negatively impacted most organisms, from insects to birds and bats (Mineau and Callaghan, 2018; Sánchez-Bayo, 2011). Several multivariate and correlative statistical analyses confirm that the impact of pesticides on biodiversity is larger than that of other intensive agriculture practices (Fuentes-Montemayor et al., 2011; Gibbs et al., 2009; Mineau and Whiteside, 2013), though some authors continue to emphasize habitat and climate changes (Fox, 2013). Hallmann et al. (2017) demonstrated that 80% of the flying insect biomass losses in Germany was not caused by increases in agricultural land, deforestation, urbanisation or climate change but instead by an unknown factor, which the authors believe is pesticide use. This is even more evident for aquatic environments, where pesticide residues from agricultural and urban runoff are the major cause of biodiversity declines at all taxa levels (Beketov et al., 2013; Weston et al., 2014).

Apart from pesticides, the introduction of synthetic fertilisers early in the 20th century is recognised as a key driver of pollinator losses in the U.K. and Europe (Ollerton et al., 2014), particularly among specialist bumblebees. In terrestrial ecosystems, the diversity of plants and associated insect populations correlates negatively with nitrogen input (Öckinger et al., 2006; Pollard et al., 1998; van Swaay et al., 2006). Aquatic species such as dragonflies have also been affected by the eutrophication of surface waters, caused by excessive fertiliser use in rural areas (Kalkman et al., 2010). Equally, anoxia due to eutrophication by fertiliser and sewage has been linked to the depletion of Chironomidae, Trichoptera and Ephemeroptera in lakes (Jenderedjian et al., 2012).

The acidification of waters in Sudbury (Ontario, Canada), as a consequence of reckless mining and smelting activities since the 1850s, has inflicted direct and indirect impacts on aquatic insect communities: mayflies were eliminated in streams with pH below 5.5, but some Odonata and Diptera species increased in numbers due to lack of fish predation (Carbone et al., 1998). Acidic waters, nevertheless, reduce the abundance of Diptera (Ceratopogonidae, Chironomidae), although aquatic insect communities can recover slowly after neutralization and recolonization.

The impact of industrial chemicals (e.g., heavy metals, persistent halogenated hydrocarbons) on insect populations has not been adequately studied. Sub-lethal effects of metal pollution on moth larvae have been reported in Europe (van Ooik et al., 2007), but its link to population-level impacts is not well established. There is consensus, however, that global declines of stoneflies, mayflies and caddisflies can be ascribed to man-made pollutants discharged into streams and rivers (Aubert, 1984; Bojková et al., 2012). Occasionally, industrial spills have wiped out entire communities of aquatic organisms, not just insects, and their recovery has taken years of cleaning efforts (Capel et al., 1988; Giger, 2009). Nevertheless, since aquatic organisms are exposed simultaneously to mixtures of several pollutants, it is difficult to assign causality to individual toxic compounds. A weight-of-evidence approach concluded that insecticides were the most toxic to chironomids, snails and fish, whereas metals and other organic pollutants had a minor effect on those organisms (Kellar et al., 2014). Similar findings have been reported by other authors working with combinations of chromium and pesticides on honeybees: neonicotinoid insecticides were the most toxic to bees, whereas the metal had an antagonistic effect upon fungicide toxicity (Sgolastra et al., 2018).

#### 4.1.3. Biological factors

Parasites and pathogens are definitively involved in the collapse of honeybee colonies in various countries (Goulson et al., 2015) and also appear associated with the declining wild bees in North America (Thorp and Shepherd, 2005). The global spread of *Varroa destructor* mite and the small hive beetle (*Aethina tumida*) pose a real concern for the apicultural industry because they transmit viral infections (vanEngelsdorp et al., 2012). However, pathogens have historically co-existed with managed bee colonies: their recent virulence is more likely to have been fostered by the exposure of bees to pesticide-contaminated pollen and nectar (Long and Krupke, 2016) that weakens their immune system (Sánchez-Bayo et al., 2016b; Tesovnik et al., 2017).

Insect biological control has helped mitigate hundreds of harmful invasive pests worldwide, though unintended ecological impacts have been recorded for at least 10 ill-fated historical efforts (Heimpel and Cock, 2018; Hajek et al., 2016; Hoddle, 2004). The human-assisted introduction of exotic species for biological control can contribute to a decline of endemic insects through processes such as competitive displacement (Roy and Brown, 2015), or direct predation and parasitism (Boettner et al., 2008; Henneman and Memmott, 2001). Yet, few documented species extinctions can be directly ascribed to insect biological control, with such cases largely confined to vulnerable island ecosystems in the Pacific (Hoddle, 2004; King et al., 2010). In the meantime, the practice of biological control has matured over the past decades, and the necessary safeguards have now been put in place to avert the introduction of species that pose tangible ecological risk – e.g., generalist feeders or vertebrate predators (Heimpel and Cock, 2018). Although carefully selected host-specific agents might still cause minor, transient impacts, they regularly reach background population levels as their (invasive) pest targets are being suppressed. Moreover, scientifically-guided biological control can help to permanently resolve invasive species problems and protect biodiversity over extensive geographical areas (Wyckhuys et al., 2019). Hence, this practice need not be viewed as a prime threat to insect biodiversity, but should instead be embraced as a tailor-made alternative to pesticide measures for invasive species control, crop protection or habitat restoration. Biological control, as a core component of ecological intensification (Bommarco et al., 2013; Wyckhuys et al., 2013), can help cut insecticide pollution in agricultural environments, revert insect biodiversity declines and help conserve insect-feeding vertebrates.

Invasive species, on the other hand, can have major impacts on the make-up and functioning of ecosystems in both mainland and island settings (Kenis et al., 2009; Reaser et al., 2007). Ecological impacts are relatively well documented for invasive ants, forest herbivores and bumblebees, with effects on locally-occurring insect communities through trophic interactions such as predation or parasitism (Kenta et al., 2007). For some invasive species, impacts can be temporary as introduced species succumb due to poor adaptation to the novel environment (Cooling and Hoffmann, 2015), while others inflict long-lasting effects, i.e. mammals that prey on giant carabids of New Zealand (McGuinness, 2007). For multiple invasive plant and animal species, ecosystem-wide cascading effects have been reported with pervasive impacts on native insect communities (Bezemer et al., 2014). For example, a global meta-analysis revealed how in 56% cases, invasive plants had negative effects leading to a reduction in the overall abundance, diversity and fitness of different organisms, including insects (Schirmel et al., 2015). The introduction of fish predators such as the rainbow trout (*Oncorhynchus mykiss*) for economic and recreational activities in South Africa has reduced the distribution of the rare dragonfly *Ecchlorolestes peringueyi*, which is currently a threatened species (Samways, 1999). Cattle grazing and the planting of exotic trees along the rivers' edge of that country have also impacted negatively on the diversity of lotic dragonflies, which are at greater risk of extinction than their lentic relatives (Clausnitzer et al., 2009).

Many reports (13%) associate the insect declines with several ecological or life-history traits (Fig. 6). The responsible traits vary among

taxa, but some general trends appear consistently. For example, specialist species are declining at higher rates than non-specialists, because they are either most susceptible to habitat changes and losses of host plants or have lower fecundity rates – usually both traits are combined in *K*-selected species. Generalist species are by nature more adaptable to environmental change due to their broader range of host plants, food and shelter requirements, behavioural plasticity and climatic adaptability, surviving under wide-ranging conditions and often colonising vacant niches and new urbanised environments (van Strien et al., 2016).

Finally, increased predation has been suggested as a contributing factor in the decline of large dung beetles in Italy (Carpaneto et al., 2007). Over-collection of specimens has also been suggested in Japan (Nakamura, 2011), but the relative impact of these factors is comparatively minor and geographically confined.

#### 4.1.4. Climate change

The current warming trend, thought by some as the main driver of butterfly and wild bees declines (Bartomeus et al., 2011; Breed et al., 2012; Parmesan et al., 1999), might positively impact on their abundance in temperate regions as they exhibit superior thermal tolerance which - in turn - may benefit their development (Deutsch et al., 2008). In contrast, insects of tropical regions have more narrow thermal thresholds and are particularly susceptible to temperature increases. Hence, global warming has increased the populations of certain butterflies in northern Europe (Kuussaari et al., 2007), expanded their geographical distribution (Isaac et al., 2011; Stefanescu et al., 2011) and caused altitudinal shifts of certain species (Chen et al., 2011; Colwell et al., 2008), yet populations of half of the world's insects are declining counter to that trend (Gilburn et al., 2015).

Global warming has certainly reduced the range of some dragonflies, stoneflies and bumblebees adapted to cold climates and higher latitudes (Ball-Damerow et al., 2014; Jacobson et al., 2018; Tierno de Figueroa et al., 2010), negatively impacted some pollinators in Mediterranean regions such as the beetle *Mylabris nevadensis* (Stefanescu et al., 2018), and might increase the extinction risk of mountainous insect species (Menéndez et al., 2006). There is also clear evidence that climate change is reducing arthropod biomass in the rainforests of Caribbean islands (Lister and Garcia, 2018).

## 5. Conclusions

This review highlights the dreadful state of insect biodiversity in the world, as almost half of the species are rapidly declining and a third are being threatened with extinction. The information presented here refers mostly to developed countries of Europe and North America (Fig. 1) since those regions have the most comprehensive historical records that allow comparisons of biodiversity on a temporal scale.

Habitat change and pollution are the main drivers of such declines. In particular, the intensification of agriculture over the past six decades stands as the root cause of the problem, and within it the widespread, relentless use of synthetic pesticides is a major driver of insect losses in recent times (Dudley and Alexander, 2017). Given that these factors apply to all countries in the world, insects are not expected to fare differently in tropical and developing countries. The conclusion is clear: unless we change our ways of producing food, insects as a whole will go down the path of extinction in a few decades (Dudley et al., 2017; Fischer et al., 2008; Gomiero et al., 2011). The repercussions this will have for the planet's ecosystems are catastrophic to say the least, as insects are at the structural and functional base of many of the world's ecosystems since their rise at the end of the Devonian period, almost 400 million years ago.

Habitat restoration, coupled with a drastic reduction in agro-chemical inputs and agricultural 'redesign', is probably the most effective way to stop further declines, particularly in areas under intensive agriculture. For example, flower and grassland strips established at the field edge enhance the abundance of wild pollinators (Blaauw and Isaacs, 2014; Hopwood, 2008), and rotation of crops with clover boosts the abundance and diversity of bumblebees (Ekroos et al., 2014; Haaland and Bersier, 2011), which in turn boost crop yield and farm profitability. These 'ecological engineering' tactics not only favour pollinators but also conserve insect natural enemies that are essential for keeping at bay the herbivorous pest species of many crops (Dover et al., 2011; Gurr et al., 2012; Lu et al., 2015). However, for these measures to be effective, it is imperative that current pesticide usage patterns, mainly insecticides and fungicides, are reduced to a minimum as to permit a recovery of insect numbers and their associated 'biological control' services (Heong et al., 2015; Way and Heong, 1994). There is no danger in reducing synthetic insecticides drastically, as they do not contribute significantly to crop yields, but trigger pest resistance, negatively affect food safety and sometimes lower farm revenue (Bredeson and Lundgren, 2018; Lechenet et al., 2017). The judicious implementation of integrated pest management (IPM) in Europe as well as in developing countries of Africa and Asia over the years achieved similar or even greater crop yields (Furlan et al., 2017; Pretty and Bharucha, 2015; Pretty et al., 2011; Thancharoen et al., 2018). Furthermore, in many of the world's farming systems, biological control constitutes an under-used yet cost-effective means to resolve agricultural pest problems while conserving biodiversity both on-farm and beyond the field border (Wyckhuys et al., 2019).

For aquatic insects, rehabilitation of marshlands and improved water quality are a must for the recovery of biodiversity (van Strien et al., 2016). This may require the implementation of effective remediation technologies to clean the existing polluted waters (Arzate et al., 2017; Pascal-Lorber and Laurent, 2011). However, priority should be given to reducing the contamination by runoff and leaching of toxic chemicals, particularly pesticides. Only such conditions can allow the re-colonization of a myriad of discrete species that support essential ecosystem services such as litter-decomposition and nutrient recycling, provide food to fish and other aquatic animals, and are efficient predators of crop pests, aquatic weeds and nuisance mosquitoes.

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